Effect of Turbidity on the Rate of Filtration and Growth of the Slipper Limpet, *Crepidula fornicata* Lamarck, 1799 [1]

BY

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(4 Text figures)

INTRODUCTION

Most lamellibranchs and a few mesogastropods (including *Crepidula fornicata* Lamarck, 1799) obtain their food by filtering out fine particulate detritus and microorganisms suspended in the surrounding water. By ciliary action, water is drawn into the mantle cavity, passed over and through the ctenidium, and then expelled. Suspended particles are trapped in the mucus sheet which covers the ctenidium and then moved into the region of the mouth in the form of mucus strands. Here the mucus strands are either ingested as food or rejected as pseudofeces.

In addition, *Crepidula fornicata* produces a coarse mucus web across the entrance of the mantle cavity which removes the larger particles from the inhalant current. The particle-laden mucus is moved to an anterior food pouch and may also be ingested as food or rejected as pseudofeces into the exhalant current (Werner, 1953).

Owen (1966) notes that the food intake of suspension feeders is a function of the efficiency of the mucus net, the availability of food in the immediate vicinity, and the rate of filtration. Any reduction in the filtration rate would also result in a reduction of food intake, and if sustained over a period of time, would be expected to have an adverse effect on tissue growth and shell deposition. Molluscan shell growth can be used as an index of metabolic stress as physiological and environmental events are reflected in the daily deposition of the shell (Pannella & MacClintock, 1968).

Several workers have found that in concentrations of turbidity-producing substances, such as silt, Fuller's earth, kaolin, or live microorganisms, the filtration rate (and therefore the feeding rate) of bivalves is reduced and may even cease completely (Loosanoff & Tommers, 1948; Rice & Smith, 1958; Loosanoff, 1961; Davids, 1964). In the existing literature, no reference was found to the effects of turbidity on the growth or rate of filtration of a suspension feeding gastropod. Therefore, the purpose of this investigation was to: (1) determine how the shell growth of *Crepidula fornicata* is affected by prolonged exposure to various levels of turbidity in nature; (2) examine the effects of increasing concentrations of silt, kaolin, and Fuller's earth on the filtration rates of *C. fornicata*.

METHODS AND RESULTS

I. Experiment on the Effect of Turbidity on Shell Growth of *Crepidula fornicata*

Shell growth studies performed in the natural environment are ecologically significant if the variable under study can be eliminated or changed by a known quantity. The variable, turbidity, can be changed easily by a transplantation of specimens from one environment to another. Other variables are not significantly changed if the transplantation sites are chosen carefully (Rhoads & Pannella, 1970). This approach was utilized to study the effect of different levels of turbidity on shell growth of *Crepidula fornicata* over a 3-week span. Specimens were collected from Quissett Harbor, just below low mean water level, and transplanted in 2 environments of contrasting turbidity and depth. Other variables, such as temperature, salinity, etc., were not significantly different between the 2 environments.

To facilitate the field transplantation, 2 tripods were built which could be easily placed and recovered by divers. The tripods were constructed from $\frac{3}{4}$ inch galvanized pipe and coated with epoxy paint to eliminate

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any potential chemical activity with sea water that could affect the experiment. Each tripod supported 3 screened trays (45 cm length, 35 cm width) in a vertical sequence at 0 cm, 45 cm, and 75 cm above the sea floor. The vertical arrangement of trays allowed comparison of the shell growth rate at different concentrations of turbidity in one environment.

Chains of *Crepidula fornicata* were collected within 24 hours of the transplantation and kept in holding tanks until used. Just prior to relocation at the new site, the top 2 or 3 juvenile specimens of each chain were marked by notching the edge of the shell. The physical disturbance of notching not only produced a tiny gap in the shell, but also caused the mantle to retract. This resulted in the formation of a prominent disturbance band once shell deposition was resumed by the mantle. The disturbance band was used to delimit the extent of growth previous to the transplantation. Sixty to 90 notched specimens with the accompanying chains were placed in each tray.

One tripod, used as a control, was placed in an area of low turbidity on the bottom of Quisset Harbor (Figure 1) on June 28, 1969, at 11:30 a.m. in 3 m of water (mean low water). The other tripod was lowered to the bottom (15 m) of Buzzards Bay at Station 7 (Rhoads & Young, 1970) by divers on June 30, 1969, at 11:00 a.m. The site of Station 7 is the same as Station F of Sanders (1958). The station is characterized by a bottom with a high silt-clay percentage (85.5%) and a benthic fauna that is comprised of 88.4% deposit feeders and 3.5% suspension feeders (Sanders, *op. cit.*). This area was selected because of the conspicuous lack of suspension feeders and the high level of turbidity due to resuspension of bottom muds by weak tidal currents (Rhoads & Young, *op. cit.*).

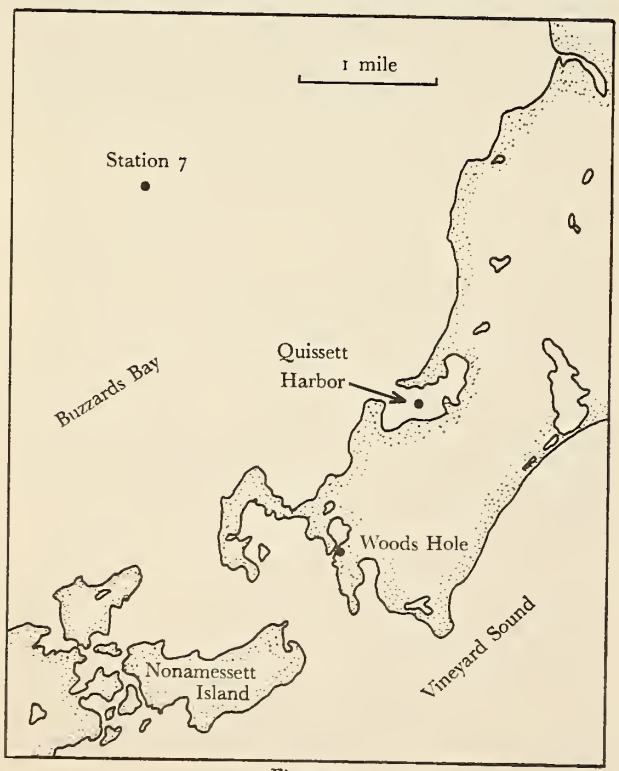

Figure 1

Map of Buzzards Bay, Massachusetts, showing the location of the transplantation sites at Station 7 (15 m) and Quissett Harbor (3 m). Sander's (1958) Station F is equivalent to Station 7 (after Rhoads and Young, 1970)

When the tripods were recovered (Quissett Harbor, 11:00 a.m., July 23, 1969; Buzzards Bay, 10:00 a.m., July 22, 1969), the animals were killed to prevent any additional shell deposition. Measurements of shell increase were made along the dorsal median of the shell with a Wild Heerburgg microscope. Growth measurements of the Quissett Harbor specimens were adjusted to 22 days of growth for comparison with the 22 days growth of the Buzzards Bay specimens.

The results of the experiment are summarized in Table 1 and Figure 2. Figure 2 illustrates that specimens in all 3 trays of the more turbid environment of Buzzards Bay transplant had a lower mean shell growth rate than those in Quissett Harbor. A definite vertical segregation in

Table 1

Comparison of shell growth in *Crepidula fornicata* at different elevations in environments of contrasting turbidity

Tray Height (cm)	n	Growth [1] Range (mm)	Mean [2] Growth (mm)	Level of Significance between Populations	% Increase versus Buzzards Bay (0 cm)
			Buzzards Bay		
0	80	0.16 - 2.16	0.79±0.05		0%
				0.1%	
45	90	0.32 - 3.04	1.23±0.05		56%
				0.5%	
75	91	0.40 - 3.36	1.56±0.05		97%
			Quissett Harbor		
0	59	0.35 - 4.37	1.74±0.10		120%
				0.1%	
45	64	0.49 - 5.98	2.52±0.13		219%
				5.0%	
75	71	0.35 - 6.47	2.91±0.14		268%

[1] Period of growth was 22 days
[2] One standard error indicated

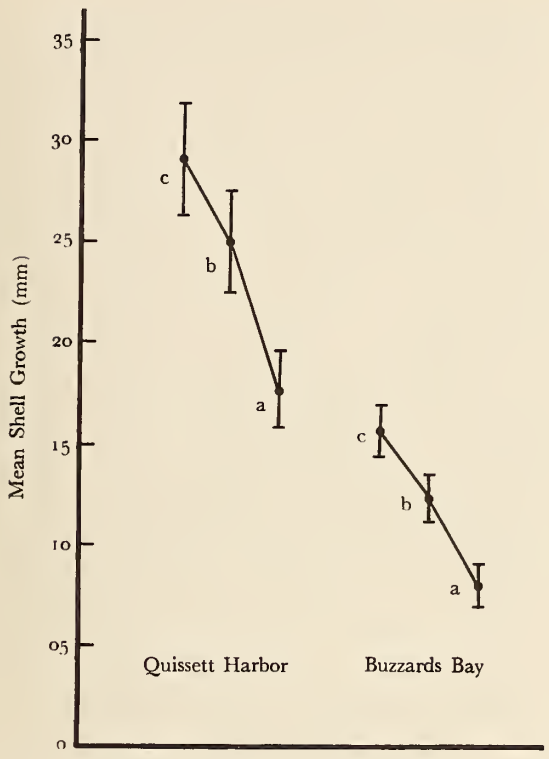

Figure 2

Growth of *Crepidula fornicata* Lamarck, 1799 in low turbidity (Quissett Harbor) versus high turbidity (Station 7, Buzzards Bay). The differential growth rates at each site correspond to elevation above the bottom: a – 0 cm; b – 45 cm; c – 75 cm (± 2 standard errors indicated)

mean growth rates was also found between adjacent trays in both environments. In each case, the highest mean growth rate was attained in the 75 cm high trays and the lowest mean growth in the trays at 0 cm. In Buzzards Bay the mean growth rate in the 75 cm tray was nearly double (97% increase) that of the 0 cm tray. In Quissett Harbor, mean growth in the 75 cm tray was an average 67% greater than the bottom (0 cm) tray. Table 1 includes values for the standard error and level of significance (two-tailed student's t test of the mean shell growth comparisons).

II. Experiment on the Effect of Turbidity on Filtration Rates of *Crepidula fornicata*

Problems dealing with growth of suspension feeders are more easily analyzed if the rate of water filtration can be measured. Many investigators have measured the volume of water transported per unit of time through the filtering mechanism of various bivalves, using either direct or indirect methods. The direct method has been used where the water from the exhalant siphon could be collected and its volume measured (Loosanoff, 1961; Coughlan & Ansell, 1964).

Due to the difficulty of measuring exhalant water discharge in most suspension feeders such as *Crepidula fornicata,* indirect methods have been developed which are based on the rate of removal of suspended particles in a solution by the filtering mechanism of the animal. The rate of water filtration is found by using Jørgensen's (1943) formula:

$$m = \frac{(\log CONC_o - \log CONC_t)\,M}{(\log e)\,t}$$

where m is the volume of water in liters transported per hour, $CONC_o$ and $CONC_t$ are the initial and final concentrations after t hours, and M is the volume of the suspension in liters.

The formula is based on the assumption that the mucus sheets retain all suspended matter from the water passed through the mantle cavity. As complete retention is unlikely, Rice & Smith (1958) note any results obtained by the indirect method will in reality be lower than actual pumping rates and therefore should be referred to as filtration rates.

Tests were conducted in the laboratory to determine filtration rates of *Crepidula fornicata* in turbid waters. Specimens were collected from Quissett Harbor and Hadley's Harbor (just below mean low water level) and transplanted in Eel Pond until needed. A 24-hour acclimatization period to the laboratory environment preceded all experiments.

Silt, kaolin (a clay-like compound), and Fuller's earth (diatomaceous earth) were used to create turbidity. Kaolin and Fuller's earth were obtained commercially while the silt was prepared from bottom mud near the tripod transplant in Quissett Harbor. The soft mud was washed with fresh water and then sieved through plankton netting to remove large particles. After settling, the water was decanted and the mud dried. The dried material was then pulverized in a mortar and rescreened (125 μ mesh) to insure relative uniformity in particle size.

Turbid solutions were obtained by placing x grams of silt, kaolin, or Fuller's earth in battery jars containing 2 liters of unfiltered sea water. The experimental concentrations ranged from 0.08 to 1.56 grams sediment per liter of water. A suspension was maintained by stirring with moderate aeration, sufficient to maintain homogeneous mixing without visibly disturbing the specimens or resuspending the heaviest particles which settled out im-

mediately. Control jars were used to determine the amount of natural clearing due to settling by gravity. With the exception of the controls, each battery jar contained 10 specimens of similar length (35 - 45 mm). New specimens were used for each concentration of silt tested. One control and 3 battery jars were used to test the effects of Fuller's earth, while 3 controls and 3 battery jars were used with kaolin, and 3 controls and 5 battery jars with silt. All experiments were conducted at 22.5 - 24.0° C.

At the commencement of each experiment and at 30 minute intervals 10 ml aliquots were taken from a uniform position in the solution (center and middepth). The concentration of turbidity in each sample was determined by measuring the percentage of light transmission with a Beckmann Colorimeter and then compared against a percentage light transmission curve obtained with known concentrations of turbidity. The experiments were terminated when the percentage of light transmission was greater than 95%.

Once the concentration in grams per liter at a given time t was known, the filtration rate was easily calculated by using JØRGENSEN's (1943) formula. However, it was necessary to use a modification of this formula because it applies only to suspensions that do not settle out. WILLENSEN (1952) gives the derivation of Jørgensen's formula which allows for settling:

$$m = M\left(\frac{\ln C_o - \ln C_t}{t}\right) - a$$

Here m is the filtration rate in liters per hour; M is the volume of the suspension in liters; C_o and C_t are initial and final concentrations at time t; and a is the proportion factor for the settling due to gravity. The control jars were used to solve for a where

$$a = \frac{\ln C_o - \ln C_t}{t}$$

The filtration rates in kaolin and Fuller's earth are represented graphically in Figure 3. Only 2 concentrations of each substance were tested. In both experiments, it was found that the filtration rate dropped sharply as the level of turbidity increased.

Figure 4 gives the filtration rates in several concentrations of silt turbidity. Here also, the filtration rate decreased in response to increasing turbidity. The sharpest reduction occurred at very low concentrations of silt (0.14 to 0.20 g per l).

DISCUSSION

The results of the transplantation experiment strongly suggest that the shell growth rate of *Crepidula fornicata*

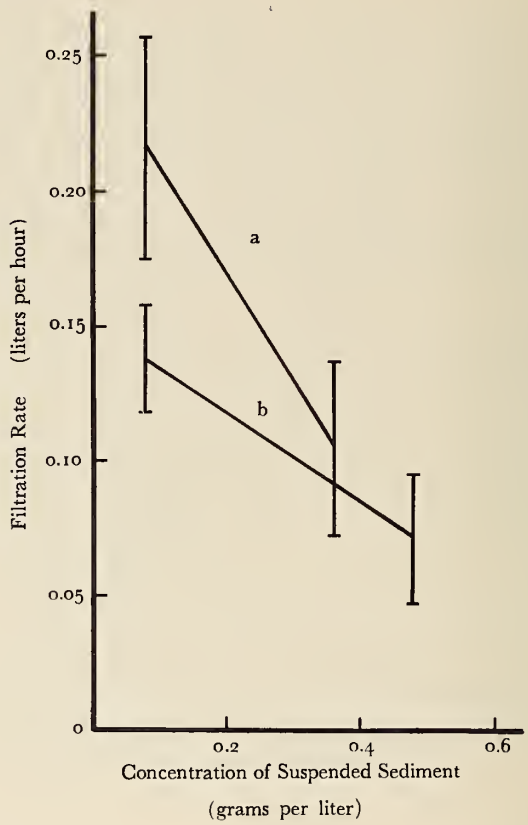

Figure 3

Filtration rate of *Crepidula fornicata* Lamarck, 1799 in kaolin (a) and Fuller's earth (b). (± 2 standard errors indicated)

is inversely related to existing turbidity levels. The rate of shell growth was seen to decrease as the level of natural turbidity increased. The zone of lowest growth at both sites was found to be at the sediment-water interface (Figure 2) where the highest level of turbidity exists in nature. RHOADS & YOUNG (1970) record similar differential growth rates of juvenile *Mercenaria mercenaria* at different elevations above the mud bottom at SANDER's (1958) Station R.

Water samples taken from the Quissett Harbor transplantation site on August 21, 1969, indicated an approximate turbidity concentration of 0.25g/l at 2 cm, 0.06g/l at 45 cm and 0.01 to 0.02g/l at 120 cm and above. The level of turbidity was determined with a Beckmann Colorimeter, using silt as the standard. These values represent estimates of the actual turbidity as microorganisms were present in the water samples. Comparable values were not obtained for Station 7 in Buzzards Bay. However, sediment traps, collecting an average flux of 15 mg

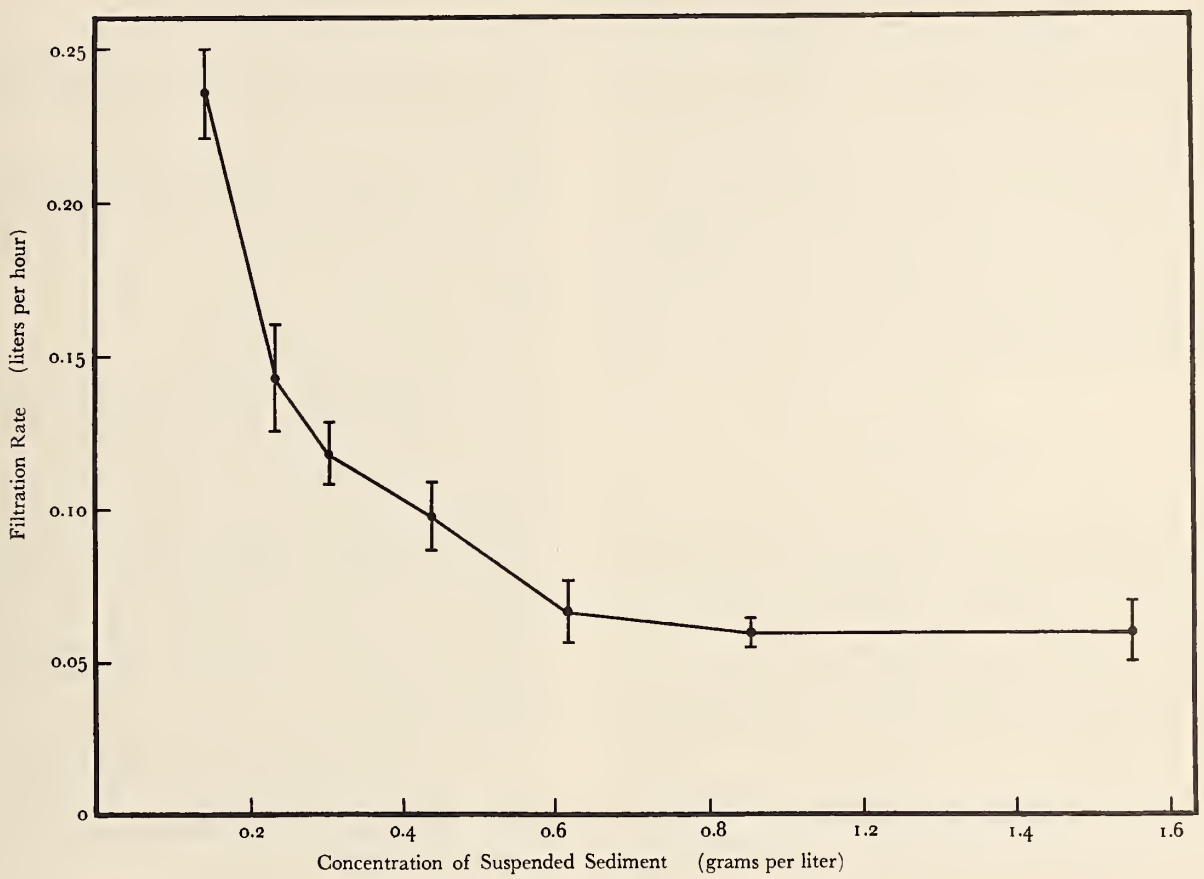

Figure 4

Filtration rate of *Crepidula fornicata* Lamarck, 1799 in silt.
(± 2 standard errors indicated)

per cm² per day (Rhoads & Young, 1970), furnish evidence of the high level of turbidity at Station 7. Rhoads & Young (*op. cit.*) note further that the turbidity is due to continuous bioturbation of the bottom muds by deposit feeders, resulting in a "fluid fecal-rich surface" that is resuspended by weak (mean 5 cm/sec) tidal currents.

Loosanoff (1961) experimentally demonstrated that concentrations of silt as small as 0.1g/l of water significantly reduced the rate of filtration in oysters. *Crepidula fornicata* exhibited the same behavior. In the concentrations of silt tested, the most significant reduction of filtration occurred between 0.14g/l and 0.21g/l (Figure 4). As noted above, similar and greater concentrations of turbidity are found existing in nature under normal conditions. Under turbid conditions similar to Station 7, the reduced amount of food intake could become a critical limiting factor in survival. This suggests that the distribution of *C. fornicata* may be regulated to a great extent by the degree of turbidity immediately above the bottom sediments.

During the course of the filtration experiments, it was also noted that the amount of pseudofeces increased as the level of turbidity increased. However, there was no significant difference in either filtration rate or pseudofeces production in silt concentrations which exceeded 0.6g/l (Figure 4). *Crepidula fornicata* can survive in highly turbid waters in the laboratory, but only by continually expelling copious amounts of pseudofeces in an attempt to keep the filtering mechanism clear of debris. An increase in production of pseudofeces would likewise interfere with normal feeding and at the same time require large amounts of energy. This type of stress in the natural environment coupled with reduced food intake, if sustained very long, would prevent effective growth of *C. fornicata*. The growth rates of the Buzzards Bay transplant support this hypothesis.

The only other variable that was significantly different between the 2 transplantation sites was depth. The Buzzards Bay transplant depth was 15 m versus 3 m at Quissett Harbor. It is possible that the transplantation from just below low tide level to 15 m of water may account for some of the reduction in growth experienced by Buzzards Bay specimens. However, *Crepidula fornicata* is commonly found distributed in Vineyard Sound down to 57 m (Summer *et al.*, 1911). Likewise, the variable depth cannot be used to satisfactorily explain the significant differential growth rates found in the vertical sequence of 75 cm at both sites. On this basis, it was concluded that turbidity was the variable responsible for limiting the growth of *C. fornicata*.

SUMMARY

1. The shell growth rate of *Crepidula fornicata* decreased as the level of natural turbidity increased. This was found to be true in a vertical sequence of 0 cm, 45 cm, and 75 cm; with the greatest turbidity and lowest shell growth at 0 cm, and lowest turbidity and highest growth at 75 cm. Likewise, shell growth was found to be greatest in a transplantation environment of low turbidity (Quissett Harbor) as compared to a high turbidity environment (Buzzards Bay).

2. The filtration rates of *Crepidula fornicata* decreased as the level of turbidity increased. Low concentrations of silt equivalent to natural levels of turbidity in nature produced significant reductions of the filtration rates. Silt, kaolin, and Fuller's earth each caused a significant reduction in the filtration rate as the concentration increased up to 0.6g/l.

3. Reduced shell growth of *Crepidula fornicata* appears to result from inadequate food intake due to clogging of the filtering mechanism by turbidity. Sustained high natural turbidity may have a limiting effect on the distribution of the suspension feeding gastropod, *C. fornicata*.

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Literature Cited

Coughlan, J. & Alan D. Ansell
1964. A direct method for determining the pumping rate of siphonate bivalves. Journ. Cons. Perma. Int. Explor. Mer. 29: 205 - 213

Davids, C.
1964. The influence of suspensions of microorganisms of different concentrations on the pumping and retention of food by the mussel (*Mytilus edulis* L.). Netherl. Journ. Sea Research 2: 233 - 249

Jørgensen, C. Barker
1943. On the water transport through the gills of bivalves. Acta Physiol. Scand. 5: 297 - 304

Loosanoff, Victor Lyon
1961. Effects of turbidity on some larval and adult bivalves. Proc. Gulf & Carib. Fish Inst. 14th Ann. Sess. Nov.; 80 - 95

Loosanoff, Victor Lyon & Frances Doretta Tommers
1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science 107: 69 - 70 (16 Jan. '48)

Owen, Gareth
1966. Feeding. pp. 1 - 51 *in* K. M. Wilber & C. M. Yonge (ed). Physiology of mollusca, vol. 2; 645 pp., illus. Acad. Press, New York

Pannella, Giorgio & Copeland MacClintock
1968. Biological and environmental rhythms reflected in molluscan shell growth. Mem. Journ. Paleo. 42: 64 - 80; 4 text figs.; 8 plts.

Rhoads, Donald C. & Giorgio Pannella
1970. The use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3: 143 - 161; 9 text figs.

Rhoads, Donald C. & David K. Young
1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. Journ. Marine Research 28: 150 - 178; 19 text figs.

Rice, Theodore & Rebecca J. Smith
1958. Filtering rates of the hard clam *Venus mercenaria* determined with radioactive phytoplankton. U. S. Fish & Wild Life Serv. Fish. Bull. 58: 73 - 82; 6 text figs.

Sanders, Howard L.
1958. Benthic studies in Buzzards Bay. I. Animal sediment relationships. Limnol. & Oceanogr. 3: 245 - 258

Sumner, Francis B., Raymond C. Osburn & Leon J. Cole
1911. A biological survey of the waters of Woods Hole and vicinity. Part 1. Physical and Zoological. Bull. U. S. Bur. Fish. 31: 1 - 442

Werner, B.
1953. Über den Nahrungserwerb der Calyptraeidae (Gastropoda, Prosobranchia). Morphologie, Histologie und Funktion der am Nahrungserwerb beteiligten Organe. Helgoländ. Wissenschaftl. Meeresuntersuch. 4: 260 - 315

Willensen, J.
1952. Quantities of water pumped by mussels (*Mytilus edulis*) and cockles (*Cardium edule*). Arch. Néerl. Zool. 10: 153 - 160